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5.

A CONTRIBUTION TO THE ANATOMY OF THE AMPHIBIAN AND REPTILIAN RETINA.

By J. W. Hulke.

After working for several years at the human retina, while seeking, in the spring of 1862, for the axial fibre described by Ritter, in the frog's rod-shaft, I became much impressed with the value of a comparative study of this coat; and meeting with H. Müller's comprehensive article on the Vertebrate Retina, in Siebold and Kölliker's Zeitschrift, I was encouraged by that great anatomist's example to commence a study which should embrace all classes of vertebrata. Having begun with the frog, I decided to continue to work upon amphibia and reptiles, intending afterwards to go back to fishes. In the autumn I communicated to the Royal Society an account of the retina of the frog, black and yellow salamander, common snake, blind worm, Spanish gecko, water and land tortoises, and turtle. A precis of this paper, necessarily very short and unillustrated, was published in the Society's Proceedings. During the past summer I have gone over much of the ground again, verifying my former conclusions in every important particular.

I now offer the readers of this journal the results of the whole investigation in these two classes of vertebrate animals. In all the species which I have examined, a uniform type of structure occurs, and this is subject to modifications which show how well founded was Müller's anticipation that a special study would bring out specific characters which would enable the anatomist, from the examination of a piece of retina, to name not only the class, but the genus and species. Enumerated in order from the choroidal surface inwards, the following layers are recognisable:—

1. Layer of rods and cones = Bacillary L. = Jacob's membrane.
2. Layer of Outer granules.

3. Inter-granule-layer.
4. Layer of Inner granules = Bowman's Nummular L. (Layers 2, 3, 4, collectively form H. Müller's granule-layers = Bowman's agglomerated granules.)
5. Granular layer = Bowman's grey vesicular matter. (I employ the first of these terms because it involves no opinion respecting the nature of the tissue.)
6. Ganglionic layer = Müller's nerve-cell L. = Bowman's caudate nucleated vesicles.
7. Optic nerve-layer.

These layers are traversed radially by the connective fibres named after their discoverer, Müller, and are collectively pervaded by an interstitial net of great delicacy, first more minutely investigated by Schultze.

Frog. Rana Temporaria (Pl. I, Fig. 1).

1.—*Layer of Rods and Cones.*

This layer contains two elements, rods and cones. In each an outer and an inner segment, separated by a bright transverse line, is discernible. The outer segment is called the *shaft,* the inner, the *body* or *appendage.*

Rods.—The shaft is a long rectangle. In isolated specimens its outer end is usually rounded, possibly from injury sustained in its separation from the choroid. Its inner end is always a straight line. The mean length of 20 shafts near the optic nerve-entrance was $\frac{1}{900}''$, the maximum, $\frac{1}{654}''$, and the mean breadth, $\frac{1}{4500}''$. Towards the front of the retina they are shorter. The appendage, or body, is a triangle or cone of variable length, always shorter than the shaft, from which the slightest force disconnects it. It is pale, and less conspicuous than the shaft, but a minute subglobular mass may sometimes be seen in its outer end, which has the same refractive power as the shaft, to the inner end of which it often remains attached in the form of a bead, when the appendage falls off. The inner, narrow end of the

appendage is always connected with an outer granule; it either expands and encloses a near granule, or contracts into a slender band, which runs to a remote granule. In this way the distance of its outer granule determines the length of the appendage. The longest of 20 measured $\frac{1}{1148}''$, many ranged between $\frac{1}{1500}''$, and some were shorter. After including the outer granule the appendage is prolonged as a pale band through the inter-granular layer. I have traced it some way amongst the inner granules, but failed to discover its final connections.

[In the perfectly fresh shaft and body no parts are distinguishable (except the minute sub-globular mass described in the outer end of the body, and the outer granule associated with the inner end of the body or its prolongation) other than a sheathing membrane, as far as I know, first described by Ritter, and a colourless contained substance. This homogeneity soon disappears, and instantly vanishes when water or chemical solutions are added. One of the first changes observable in the shafts is a fine longitudinal striation, not unlike that seen in the sarcolemma of muscle. Then the shafts take the familiar curved and hooked forms. In water or solutions of chromic acid, the shafts swell, lose their rectilinear shape, and their contents become granular, opaque, and marked by lines transverse to the axis. Strong solutions of chromic acid act similarly, but the shafts swell less, have harder outlines and a stronger transverse striation suggestive of lamination. The shafts not unfrequently split along these cross lines. When an eyeball is immersed in a solution of chromic acid, so that this acts on the rods in situ by soaking through the outer coats, different effects are observed. Here the rods assume a variety of shapes more or less rudely resembling a club or long vesicle, the swollen being the outer, the slender the inner end of the rod. The swollen part is finely granular, and sometimes, as Ritter figures, marked with lines radiating from a central spot, like the spokes of a wheel. The narrow part is usually homogeneous, and in the more vesicular forms sometimes so contracted and lengthened that it resembles a horny fibre, $\frac{1}{1800}''$ to $\frac{1}{450}''$ long, by $\frac{1}{18000}''$ broad. The slightest force disconnects the vesicle from the fibre, and sets it free as a circular or elliptical disc.

From a comparison with his figures, I believe that this fibre, which I regard as the transformed inner segment of the rod-sheath, is identical with the fibre which Ritter describes in the axis of the rod-shaft, surrounded by the other contents of the sheath in the manner of a medulla. He compares it with the axis-cylinder of nerve, regards it as the true termination of Müller's radial fibres, and considers it as valuable evidence in support of the nervous nature of the rods.*

The axial situation of Ritter's fibre has been confirmed by Manz, who considers it nervous.† Krause has also verified its existence in chromic acid preparations, but doubts its nervous nature, and even its original existence.‡

I submit that the true origin of the fibre is easily demonstrable by tracing its development through numerous intermediate phases which occur between the club-like and stalked vesicular transformations of the rods, and constitute a very regularly progressive series. Even in the club-like forms, where Ritter says its demonstration is not difficult, because the fibre is less closely embraced by the inner part of the rod and their separate outlines are better distinguishable, I have never seen the fibre pass inside the rod-sheath, its contour is always uninterruptedly continuous with that of the sheath.]

Cones.—These are flask or bulb-like objects, smaller than the rods, and placed at regular intervals amongst them. They also have an outer and an inner segment, a shaft, and a body, the junction being marked by a bright transverse line, where they are very apt to break asunder.

The shaft resembles a diminutive rod-shaft, but differs from it in tapering slightly towards its outer end, in being rather more persistent, and in shrinking less in chromic acid The body, larger than the shaft, is flask-shaped. Its outer end, narrow and truncated, contains the well known pale yellow bead, which lies just inside the line that marks the junction of body and shaft. Its inner end is connected with an outer granule, in the same manner as we have seen the

* Ritter A. f. O. Bd. V, Abth., ii S. 101. Taf. 4, F. 1—26.

† Manz. Henle w. Pfeuffer's Ztschr., 3 R., Bd. X., Taf. viii, S. 301.

‡ Krause. Henle w. Pfeuffer's Ztschr., 3 R., Bd. xi., S. 175.

corresponding part of the rod is. The mean length of several fresh cones near the optic nerve was $\frac{1}{1333}''$, and that of others in a chromic acid preparation from the same region $\frac{1}{1548}'$. Like the rods the cones consist of a sheathing membrane, and an albuminous contents.

Relations of the Bacillary Elements with other Tissues.—The rods and cones are insulated by processes of dark pigment prolonged from the inner surface of the choroid. In successful sections, where their relations have been little disturbed, they reach to the line marking the union of shaft and body. The pigment occurs in grains which are linked in a linear series by a soft transparent substance, or are closely applied to transparent fibres.

In vertical sections of hardened retina, a clear sharp line is discernible between the bacillary and the layer of outer granules. The retina readily splits along this line; it is the edge of a fenestrated homogeneous membrane, first correctly described by Schultze, and named by him the Membrana limitans externa.* Its apertures receive the inner ends of the rod and cone bodies. It will be again referred to in the description of the connective frame.

[Hanover, so far as I know, first observed and figured the division of the rods and cones into an outer and an inner segment, but fell into the mistake of supposing that the tapering inner segment of the rods was directed outwards towards the choroid, an error the more singular that he placed the cone-shafts, which are homologuous with the rod-shafts, correctly.† Bowman, whose masterly researches marked a new era in the history of the retina, in 1847, described the cones as "globular, or egg-shaped, and sometimes to have a small blunt spur upon them, turned towards the choroid." With Hanover, he thought that the pointed extremities of the rods were imbedded in the choroidal epithelium.‡ Vintschgau has curiously misunderstood the relations of the rods and cones, placing them upon one another

* Schultze. Observationes de Retinæ Structura penitiori. Bonnæ, 1859

† Hanover. Recherches Microscopiques sur le Systeme Nerveux. 1844.

‡ Bowman. Lectures on parts concerned in the operations on the eye London, 1849.

in a double series.* H. Müller especially (whose recent death is a heavy loss to histology) and Kölliker clearly described their segmentation, and their connection with the outer granules.†]

2. *Layer of Outer Granules.*

The *outer granules* are round or roundly-oval cells, from $\frac{1}{2500}$ to $\frac{1}{3700}$ of an inch in diameter. They have a distinct, bright, central nucleus, and form a thin layer of two or three rows. Each is associated with a rod or cone, in the manner already described, so that their number equals these, and each appears, at its opposite pole, to send a fibre inwards. This is really a prolongation of the inner end of the rod, or cone-body.

3. *Inter-granule-Layer.*

Placed between the outer and inner granules this appears in vertical sections as an inconspicuous line. Schultze pointed out that a high power resolves it into a web of fibrous tissue. It is traversed by Müller's (connective) radial fibres, and by the fibres prolonged beyond the outer granules from the rod and cone-bodies.

4. *Layer of Inner Granules.*

The inner granules, like the outer, are well defined cells. In chromic acid preparations three kinds are distinguishable. 1. Small, subglobular, polygonal cells or nuclei, ranging between $\frac{1}{4500}$ and $\frac{1}{6000}$ of an inch in diameter. These are more numerous; carmine imparts to them a deeper stain; they are less granular in texture, and their refractive power is higher than that of the other cells. 2. Large round, or roundly oval cells, from $\frac{1}{1800}''$ to $\frac{1}{2700}''$ in diameter. These

* Vintschgau. Richerche sulla struttura microscopica della Retina del Uomo, degli animali vertebrati, e dei Cephalopodi. Sitzungs Berichte der Akademie der Wissenschaften. Wien. Bd. xi, S. 943—977.

† Müller. Anat. Phys. Untersuch. über die retina beim Menschen u. Wirbelthieren. Ztschr. f. Wiss. Zool. Siebold u. Kölliker. Bd. viii, Hft. 1. 1856.

are most abundant in the inner part of the layer, near the granular layer, and are not unlike some ganglionic cells. 3. Large sub-oval cells, closely connected with Müller's (connective) radial fibres by a fine filamentous tissue, noticed by Schultze. These have been figured by some observers as nodes or nuclei in the radial fibres.

5. *Granular Layer.—Grey Nervous Layer.*

This has about the same thickness as the layer of inner granules.

From its resemblance to grey cerebral matter when examined with a low magnifying power, it was generally recognised as such until Schultze demonstrated that it is a sponge-like substance, composed of a closely-woven web of exceedingly delicate fibrous tissue, partly drawn from Müller's (connective) radial fibres. To make out the real structure a high power is required, and the thinnest part of chromic acid sections should be chosen. Crossing the layer, in a direction perpendicular to its extension, are Müller's (connective) radial fibres, and optic nerve fibres may be followed outwards for some distance in it. I have failed to distinguish the exceedingly fine and almost innumerable nervous filaments which Schultze describes clothing the connective web.

6. *The Ganglion-cell-Layer.*

Near the optic nerve the ganglion-cells, three or four deep, form a continuous bed between the granular and the optic nerve layers. The outermost cells are partly imbedded in the granular layer. They become less numerous with increasing distance from the optic nerve-entrance, and, in the front of the retina, are scattered at intervals in the meshes of the optic nerve. Two forms are distinguishable: 1. Polygonal cells, from $\frac{1}{3000}$ to $\frac{1}{4500}$ of an inch in diameter, to which carmine gives a deep stain. These detach pale filaments, comparable with the axis-cylinder of nerve; some of

them connect themselves with similar filaments from neighbouring cells, others join the optic nerve-bundles, and a third set run outwards into the granular layer. The filaments have single outlines, but with $\frac{1}{25}''$ object-lens a double contour, suggestive of an enclosing membrane may sometimes be demonstrated in the cells. 2. Round and roundly oval cells, from $\frac{1}{2500}''$ to $\frac{1}{1800}''$ in diameter, taking a less deep tint from carmine, and some containing a large, usually excentric nucleus.

7. The Optic-Nerve Layer.

After piercing the sclerotic and choroid, the optic nerve forms a slightly raised circular disc, from which flat bundles of fibres radiate on all sides, repeatedly dividing and combining in a plexiform manner, and decreasing in number as they approach the front of the retina. They detach fibres from their outer surface at a sharp curve, which I have traced some way into the granular layer, without seeing their termination. The connection of the opticus-fibres with the ganglion-cells has been mentioned. The fresh fibres show fewer and less conspicuous varicosities, and their size is more uniform than in the chelonia. In chromic acid preparations they have sharp single outlines, without any indication of a medulla.

Connective Frame.

This structure retains the several layers in their order, fixes the elementary tissues in their layers, and, in a word, preserves the orderly arrangement of all the parts of this wonderfully complex coat. It is divisible into three principal segments:—1. A membranous expansion at the inner surface of the retina, named the membrana limitans interna; 2. a fenestrated membrane bounding the inner surface of the bacillary layer, the membrana limitans externa; and 3. an intermediate system of ties, named after their discoverer, Müller's radial fibres

1. The membrana limitans interna, as its name implies, limits the inner surface of the retina ; no indications of structure are discernible in it. Its outer surface gives origin to the radial fibres, and its inner surface is in contact with the hyaloid capsule of the vitreous humour. 2. The membrana limitans externa has been already mentioned in connection with the bacillary layer. It resembles the membrana limitans interna in its physical and chemical characters, but differs from it in being fenestrated. Schultze not inaptly compares it, with the rods and cones sitting in its apertures, to an egg-board* with eggs. 3. Müller's radial fibres spring by expanded membranous roots from the outer surface of the membrana limitans interna. They pass through the meshes of the optic nerve-bundles, and contracting form stout conspicuous fibres which have hard outlines, and a peculiar, stiff, horny-looking character. These pass outwards in a radial direction perpendicularly through the intervening layers, dividing and subdividing, becoming more and more attenuated, and finally reach the inner surface of the membrana limitans externa, where they end. In the granular layer they are often indistinct, and sometimes disappear. This Schultze and Manz explain by a sudden and complete dehiscence of the fibres, and their transformation into the spongy filamentous tissue proper to this layer. I do not doubt that their branches contribute to this tissue, but I have so frequently traced the trunks uninterruptedly through this layer (unless they had been snapped, in which case their ends are usually visible), that I incline to think they all pass through it, and would attribute their occasional disappearance to their dipping from the surface of the section, and to the high dispersive power of the sponge-like tissue. In the layer of inner granules, they resemble strong pillars, between which the cells are piled in vertical series. They detach innumerable filaments of extreme tenuity, which spin a delicate web about the cells, maintaining their arrangement. In

* A board pierced with round holes, in which eggs are stored upright for winter use.

some preparations glassy membranes appear to span the forks of the primary divisions. These have been figured by Schultze. The points of division sometimes exhibit fusiform swellings, and similar nodal thickenings occur in the continuity of the fibres, especially near the intergranular layer. Their texture is identical with that of the radial fibres, and they do not exhibit anything like a nucleus. Passing outwards from the inner granules, some of the fibres lose themselves in the intergranular layer contributing to it, whilst others proceed between the outer granules to the membrana limitans externa as mentioned above.

Widely different opinions have prevailed respecting the connections and nature of the radial fibres. H. Müller, their discoverer, and Kölliker at first confounded their terminal branches with the prolongations from the rods and cones (to which Kölliker now proposes to restrict the name Müller's fibres), and missed their termination in the membrana limitans externa. They regarded them as truly nervous, and thought they had found in them the missing link between the rods and cones on the one side, and the ganglion cells and nerve fibres on the other side of the retina. This was opposed by Schultze, who showed the distinctness of Müller's radial from the rod and cone-fibres, and their connection with the homogeneous limiting membranes. He rightly judged them to be modified connective tissue, and assigned them a purely mechanical office. Schultze's views were subsequently adopted by H. Müller and Remak, and by Kölliker with some reservations concerning the roots of the radial fibres, and the connective-tissue-nature of the membrana limitans interna.

Blood-vessels.

No blood-vessels are to be met with in the frog's retina, a fact pointed out by Müller and Hyrtel. The vascular system in the hyaloid capsule of the vitreous humour, which is in contact with the membrana limitans interna, and the intimate relation subsisting between the bacillary layer and the choroid, are probable compensations for this want.

To avoid repetition, I may say that I have not found blood-vessels in any amphibian or reptilian retina.

Black and Yellow Salamander.

1. *Bacillary Layer.*

The rods closely resemble those of the frog; the shaft, I think, is rather larger. The triangular or conical appendage always contains its outer granule, beyond which it runs inwards through the inter-granular layer in the form of a delicate pale band, very difficult to distinguish from the finer branches of Müller's connective fibres. The shafts are insulated by prolongations from the inner surface of the choroid, and the appendages sit in apertures in the membrana limitans externa.

2. *Layer of Outer Granules.*

The outer granules are large, round, and roundly-oval cells, with an average diameter of $\frac{1}{1800}''$ in chromic acid preparations. Near the optic nerve they lie in three rows. Their connection with the rods has just been mentioned.

3. *Intergranular Layer.*

This is a narrow, inconspicuous band of closely-woven fibres, in part derived from Müller's radial fibres which traverse it. It also transmits the bacillary fibres on their inward passage.

4. *Layer of Inner Granules.*

The inner granules are also round, or roundly-oval cells, in chromic acid preparations frequently polygonal. They have an average diameter of $\frac{1}{2250}''$, and are smaller than the outer granules from which they are also distinguished by their higher refraction. They are packed between the radial connective fibres. Besides these, most sections exhibit a few larger, more uniformly circular cells of lower refraction, and

scarcely stained by carmine. Near the inner surface of the layer a third kind occurs, always, I think, associated with Müller's connective radial fibres. These are pale finely granular, shuttle-shaped cells, averaging $\frac{1}{600}''$ in length by $\frac{1}{3000}''$ in breadth. They are closely connected with the radial fibres, but are not nodal swellings of them.

5. *Granular Layer.*

A closely-woven, fibrous web continuous with Müller's connective radial fibres, and contributing to the connective frame in the layer of inner granules.

6. *Layer of Ganglion-Cells.*

The ganglion-cells are round, roundly-oval, polygonal and multipolar. Some attain a diameter of $\frac{1}{1800}''$, a few slightly exceed this, and many are below it. I have traced processes from them to the opticus-bundles. Carmine stains some cells deeply, others scarcely at all.

7. *Optic-nerve-Layer.*

Even near the optic nerve-entrance this forms only a thin layer. The meshes are traversed by the roots of the radial fibres.

Connective Frame.

This agrees with that of the frog's retina too closely to require a separate description.

Blood-vessels.

No blood-vessels penetrate the salamander's retina.

Natrix Torquata (Pl. I, Fig. 3).

1. *Bacillary Layer.*

This is composed of long flask-shaped bodies surmounted by a smaller, slender shaft, which generally breaks away and remains buried in the choroid when the retina is detached.

In the body, an outer and an inner part are discernible; the latter is always connected, either by inclusion or by an intermediate band, with an outer granule. The coloured beads, so conspicuous in frog, turtle, tortoises, blindworm, and some lizards, do not occur in the common snake.

I am uncertain whether these elements should be regarded as rods or cones. Some are longer and more slender than others, and if the stouter are regarded as cones, the slender may be looked upon as rods.

2. *Layer of Outer Granules.*

The granules are large circular nucleated cells, each of which is always associated with a bacillary element. In my best sections I have found only one row of cells, so that the thickness of the layer was less than in the frog and tortoises.

3. *Inter-granular Layer.*

A closely-woven web, stretched concentrically with the layer of outer granules. The layer is thicker, and the fibres composing it are stouter than in the frog and tortoises. Small fusiform swellings occur sparingly in the fibres. When the retina splits at the inner surface of this layer, it remains with the outer granules, from which it would appear that the layer is more closely connected with these (strictly with the bacillary sheaths in which they lie) than with the inner granules.

4. *The Layer of Inner Granules.*

These granules are large round granular cells. They lie in several rows amongst the connective radial fibres. The thickness of the layer nearly equals that of the granular layer.

5. *The Granular Layer.*

Its structure agrees with that of the other reptiles described. Its derivation, in part, from the connective radial fibres is evident.

6. *The Ganglion-Cell-Layer.*

The cells are mostly round, or roundly-oval. I have traced filaments passing between them and the optic nerve-bundles.

7. *Optic Nerve-Layer.*

The anatomical characters and distribution of the optic nerve-fibres do not exhibit any special features.

Connective Frame.

The membrana limitans interna, and externa essentially agree with those of other reptiles. The greater strength of the inter-granule-layer has been noticed. The connective radial fibres arising from the membrana limitans interna are very slender. They are easily traceable to the inter-granule-layer, where most of them disappear.

Anguis Fragilis. Blind-worm.

1. *Bacillary Layer.*

This contains both rods and cones. In each an outer and an inner segment, a shaft and a body are discernible; and in each the body is divisible in two parts, separated by an intermediate bright band.

Rods.—These are long, slender, flask-like objects. The bodies greatly exceed the shafts, which are very diminutive.

Cones.—These are more club-shaped, and stouter than the rods. The outer end of the cone-body contains a pale green bead.

2. *Layer of Outer Granules.*

The granules are large round cells, each of which is included in the inner segment of a rod or cone, or in a prolongation from it, which is continued inwards beyond the cell in the form of a pale fibre. The cells lie in two or three rows.

(The inner granules and granular layer do not present any special features).

5. *Ganglion-Cell-Layer.*

Multipolar cells are numerous. I have frequently seen communications between them and the optic nerve fibres.

Spanish Gecko (Pl. I, Fig. 4).

1. *Bacillary Layer.*

In the gecko the bacillary element is divisible into shaft and body, as in other lizards. The shaft is a large, long rectangle, nearly equal to that of the frog. The body much paler, of lower refracting power, and softer outline than the shaft, is a large, stout, flask-shaped object. Its inner end contains an outer granule, and, passing through the membrana limitans externa, runs inwards, as a delicate fibre, which is traceable with extreme difficulty through the inter-granule-layer.

Chromic acid acts on the bacillary shaft in the same manner as it does in the frog. It solidifies the contents of the bacillary body, which form a dark granular mass in the outer end of the body, bounded towards the outer granule by a bright homogeneous band, which takes a deep stain from carmine. The membrana limitans externa lies in the level of this band.

The shafts are insulated by the choroid, which dips in between them to the line marking their union with the bodies.

2. *Layer of Outer Granules.*

The large round nucleated cells which compose this layer are disposed in a single row, each lying in the inner end of a bacillary body, just inside the plane of the membrana limitans externa.

3. *Inter-granule-Layer.*

A web of nucleated fibres, of inconsiderable thickness, connected with the connective radial fibres.

4. *Layer of Inner Granules.*

This is nearly as thick as the granular layer, and three times as thick as the layer of outer granules. It consists of round and polygonal cells, which are smaller, and which receive a deeper stain from carmine than the outer granules. No nucleus is discernible in them. They are packed in an areolar tissue derived from the connective radial fibres, and at the thinnest parts of good sections, an exceedingly fine web drawn from the areolæ is seen to surround them.

5. *Granular Layer.*

This is a close, solid web, drawn in great part from the connective radial fibres, and itself contributing fibres, which reinforce the radial system in the layer of inner granules.

6. *Ganglion-Cell-Layer.*

The cells are mostly multipolar. Their limbs communicate freely with the optic nerve-bundles, and some run outwards into the granular layer.

7. *Optic Nerve Layer.*

The optic nerve pierces the sclerotic very obliquely. Its bundles gain the retina by perforating the base of a conical brownish black pecten which rests on the lamina cribrosa, and projects about 1‴ into the vitreous humour. The recent nerve fibres exhibit frequent varicosities. In stained chromic acid sections I have a few times traced nerve fibres nearly to the outer surface of the granular layer.

Connective Frame.

The membrana limitans externa, and interna resemble those of other reptiles, and do not require particular description. The radial fibres arise from the membrana limitans interna by very expanded roots, and are stout and pillar-like in the ganglionic and inner half of the granular layer. They contribute largely to the tissue of this layer, and divide at acute angles near its outer surface into two or three branches which proceed to the layer of inner granules, where, reinforced by other fibres taking their origin in the granular layer, they form areolæ, which lodge inner granules. A few fibres can be traced uninterruptedly from the point of division of the trunks in the granular layer to the inter-granule-layer, where they, together with other fibres derived from the framework of the layer of inner granules, are lost.

TESTUDO GRÆCA.—(LAND TORTOISE.)

This retina closely resembles that of the turtle on a small scale.

1. *Bacillary Layer.*

Rods and cones both occur. The large size of its body, and the small proportion of its shaft, give the rods a somewhat cone-like appearance. They are best distinguished from the cones by the absence of the coloured bead, which characterises these. Both consist of a shaft imbedded in the choroid, and a body, the inner end of which rests in the membrana limitans externa, and is either rounded and includes one of the outer granules, or is shuttle-shaped and prolonged inwards in the form of a pale band to meet a more remote outer granule. The rods are club-shaped. The shaft is a slender rectangle, of much higher refracting power than the thicker club-like body. The cones resemble the rods in shape, but contain a coloured bead, which lies in the outer

end of the cone-body. Two kinds occur: 1. Larger cones enclosing a ruby bead. 2. Smaller cones, containing a pale yellow bead. The cone-shaft resembles a small rod-shaft. In perfectly fresh cones (taken from an eye immediately after decapitation), I have remarked a difference in the outer and inner half of the cone-body, the former being dark, and the latter pale and more transparent.

2. *Layer of Outer Granules.*

This is composed of two rows of round, clear, cells, about $\frac{1}{4500}''$ in diameter, with a small, bright, usually central nucleus. Each cell is associated with a rod or cone, and each appears to send a pale fibre inwards, which is really prolonged from the rod or cone. This fibre, more delicate than that which passes between the rod or cone and the outer granule, is with difficulty traceable through the inter-granule layer, but I have a few times followed it for some distance amongst the inner granules.

3. *The Intergranule Layer.*

A fibrous web of inconsiderable thickness. In the delicacy of its fibres it resembles the intergranule-layer of the frog more than that of the turtle.

4. *The Layer of Inner Granules.*

The inner granules are circular cells rather larger than the outer granules. They have no nucleus, and in chromic acid preparations are coarsely granulated. Behind the equator they lie between the radial fibres three or four deep. In addition to these cells the layer contains bipolar oblong bodies, with a peculiar granular and somewhat translucent texture. These are closely applied to the radial fibres, and from each end prolong a pale band upon them. I have traced the outer prolongation through the intergranule to the outer granule-layer, but without finding its termination. There is no structural continuity between these bipolar

bodies and the radial fibres, to which they are merely bound by a fine fibrous web.

5. *Granular Layer.*

A sponge-like fibrous web, traversed by the connective radial fibres, from which it is in part derived, and by other fibres, also having a radial direction, which come from the ganglion-cells. I have also traced fibres in it to the optic nerve-bundles.

6. *Ganglionic Layer.*

The ganglion-cells are—1. Large, pale, multipolar cells, with single outline and finely granular texture. They contain a conspicuous central nucleus, and sometimes a nucleolus, and communicate with neighbouring cells and with the optic nerve bundles. They also send filaments into the granular layer. 2. Free nuclei resembling those just described. These are more numerous than the multipolar cells

7. *Optic Nerve-Layer.*

Fresh nerve fibres present many varicosities. In a few I have seen a double outline.

Connective Frame.

The structure and relations of the limiting membranes are identical with those of other chelonia. The radial fibres closely resemble those of the Terrapene Europea.

WATER-TORTOISE—TERRAPENE EUROPEA.

The retina of the European water-tortoise on a small scale has a very close general resemblance to that of the turtle.

1. *Bacillary Layer.*

Rods and cones are both present. They are very like those of the turtle.

Rods.—The shafts are much smaller than the bodies, from

which they generally break in removing the fresh retina for examination. The bodies contain, or are connected by an intermediate band with the outer granules.

Cones.—These contain bright coloured beads. Three kinds may be distinguished. 1. Large ruby-beaded cones. 2. Smaller yellow-beaded cones. 3. Pale green-beaded cones, generally, but not always, smaller than those with yellow beads, and never as large as those with ruby beads. The yellow-beaded cones were regarded by Hanover as rods. The cone-shafts are more slender than the rod-shafts, and taper slightly outwards. The coloured bead always lies in the outer end of the body, with the inner end of which an outer granule is always associated. The rods and cones are insulated by pigmental prolongations of choroid.

2. *Layer of Outer Granules.*

This is composed of two, or at most, three rows of circular cells, which are clearer and rather smaller than the inner granules. Their nucleus is less distinct than in the corresponding cells in the turtle. Each outer granule is associated with a rod or cone, and a pale fibre is prolonged inwards from the rod or cone body, which appears to proceed from the outer granule included in it. In consequence of its low refracting power and extreme delicacy, this fibre is very difficult to follow, and I have not yet succeeded in tracing it through the intergranule-layers. In chromic acid preparations the outer granules included in the rod and cone-sheaths are sometimes metamorphosed into rhomboidal or elliptical objects, the inner ends of which dilate and form minute triangles where they touch the outer surface of the intergranule-layer.

3. *Intergranule-Layer.*

The fibrous tissue of this layer is very much finer than that of the turtle, and nearly resembles that of the land-tortoise. It receives accessions from the connective radial fibres.

4. *Layer of Inner Granules.*

This is more than twice as thick as the layer of outer granules. The cells are round, or roundly-oval, and rather smaller than the outer granules. Their outline is sharp, their texture is coarsely granular in chromic acid preparations, and they want a distinct nucleus. In addition to these cells this layer contains the fusiform bodies associated with the radial fibres, which are more particularly described in Testudo Græca.

5. *Granular Layer.*

This is a close sponge-like web, derived partly from the connective radial fibres which traverse it.

6. *Layer of Ganglion-Cells.*

Two kinds of ganglion cells are distinguishable. 1. Pale, finely-granular, multipolar cells with a faint single outline. They contain a large round or roundly-oval nucleus, which has a strong double outline like that of a membranous wall, and a coarsely granular appearance. 2. Free, round or roundly-oval nuclei (or cells) like those in the multipolar cells just described. These are most numerous. The multipolar cells detach fibres which are distributed similarly to those in the turtle.

7. *Optic Nerve-Layer.*

Varicosities are common in the fresh nerve-fibres. Some fibres are broader than others, and exhibit a strong, dark outline suggestive of medulla.

Connective Frame.

The membranous roots of the radial fibres are repeatedly cleft, which gives them a more fibrous appearance than in the turtle. The outer part of the granular layer gives origin to stout fibres, which proceed radially with those which have traversed this layer to the membrana limitans externa.

Edible Turtle. Chelonia Mydas (Pl. I, Fig. 2).

1. *Bacillary Layer.*

Both rods and cones are present. They greatly exceed those of the frog in size. In each a shaft and a body separated by a bright transverse line are discernible.

Rods.—The shaft is a long rectangle, resembling, but rather smaller than that of the frog. Near the optic nerve the mean length is about $\frac{1}{1500}''$, and the mean breadth $\frac{1}{6000}''$. The body is club-shaped, and much larger than the shaft, the reverse of that which obtains in the frog. The narrow end, joining the shaft, is truncated. The swollen end directed inwards is rounded, and incloses one of the outermost of the outer granules, or it tapers to a band which proceeds inwards to a more remote lying outer granule. A distinct sheath is easily distinguishable in both shaft and body, in fresh as well as in specimens hardened by chromic acid. It is stout in the shaft and exceedingly delicate in the body. The contents of the outer half of the body are finely granulated, which makes this part less transparent than the inner half of the body; and the darker part is bounded inwards by a bright band, between which and the outer granule lying in the inner end of the body, a clear space is sometimes visible.

Chromic acid, acting on the rods *in situ*, develops Ritter's fibres. They resemble those of the frog, and are clearly metamorphosed rod sheaths.

Cones.—These are smaller than the rods, from which they are also distinguished by their bright coloured beads. The shaft is a repetition of the rod-shaft on a smaller scale. The body is a large club-shaped vesicle. Its outer end always contains a conspicuous coloured bead which lies close to the transverse line dividing shaft and body. Its inner end always incloses or is connected by an intermediate band with an outer granule in the same manner as the corresponding parts in the rods.

According to their size and the colour of their bead, the cones fall into three classes. 1. Large cones, near the optic nerve about $\frac{1}{643}''$ long, containing a *ruby* bead averaging $\frac{1}{3857}''$ in diameter, which iodine changes to a deep mauve colour. 2. Smaller cones, about $\frac{1}{750}''$ long, or rather less. They contain a yellow bead which is smaller than the ruby beads, and is turned green by iodine. 3. Still smaller cones with a pale green bead. The ruby cones are the most, the green-beaded cones the least, numerous. In the region around the optic nerve I have collected in one field as many as 56 ruby to 36 yellow-beaded cones.

Relations of the Bacillary Elements to other Structures.—The rods and cones are insulated by pigmented processes sent in between them from the inner surface of the choroid in the same manner as in the frog. Their relations to the membrana limitans externa is also similar. The inner end of the rod- and cone-body, or its connecting band, after inclosing the outer granule, as described above, is prolonged inwards in the form of a very fine, pale, varicose fibre. I have traced this through the inter-granule and inner granule-layers for a considerable distance in the granular layer, but have not seen its termination. Its resemblance to the axis-cylinder of nerve is striking.

2. *Layer of Outer Granules.*

This consists of two or three tiers of clear, round cells from $\frac{1}{2000}''$ to $\frac{1}{3000}''$ in diameter. They have a small, bright central nucleus, and are always associated with a rod or cone.

3. *Inter-Granule-Layer.*

This is a conspicuous fibrous web much thicker than in the frog. It consists of large and small fibres. The largest are flat bands some $\frac{1}{8000}''$ broad, homogeneous, or exhibiting a faint longitudinal striation. They repeatedly divide and sub-divide till the smallest resulting filaments are less than $\frac{1}{18000}''$ wide. The great meshes between the larger fibres are filled with closer nets composed of the finer fibres.

The layer gives passage to the fibres prolonged inwards from the rods and cones, as well as to radial fibres belonging to the connective frame, by which it is reinforced. It is a modified connective tissue. H. Müller regarded the fibres as the long branching limits of large multipolar cells, I think on insufficient evidence, and he suggests that they may be the objects described by Bowman as ganglion cells.*

4. *Inner Granule-Layer.*

This is two or three times as thick as the layer of outer granules. The inner granules are round cells with a distinct wall, from $\frac{1}{4500}''$ to $\frac{1}{3000}''$ in diameter. Their contents are coarsely granular; no distinct nucleus is observable. They are packed in areolæ formed by the connective radial fibres, and are surrounded by delicate filaments derived from these.

5. *Granular Layer.*

Nearly as thick as the layer of inner granules, the granular layer consists of a very closely-woven web of exceedingly fine fibrous tissue. It owes its granular appearance in sections to innumerable ends of divided fibres. Its derivation, in great part, from the connective radial fibres is more easily demonstrated in this than in any other retina which I have examined.

6. *Ganglion-Cell-Layers.*

The ganglion-cells lie between the granular layer and that of the optic nerve, the outermost being imbedded in the granular layer. They are large, polygonal, multipolar cells of low refracting power; have a finely granular appearance, and contain a conspicuous nucleus, which sometimes is nucleolated. Their limbs branch, and some of the resulting fibres join those of neighbouring cells, others mix with the optic nerve fibres, and a third set penetrate the granular layer. I have traced these last to a point in this layer

* Müller. Zschr. f. wiss. Zool., Bd. viii. Taf. 1, F. 14.

beyond that to which I have traced the rod and cone-fibres coming from the opposite direction.

Besides the multipolar, there are roundish cells or nuclei identical in appearance with the nuclei of the multipolar cells. They are more numerous than these last, and they sometimes have ragged masses of a finely granular substance sticking to them, which may be portions of disintegrated cell. Müller notices this.

7. *Optic Nerve-Layer.*

The optic nerve pierces the thick cartilaginous sclerotic very obliquely. The bed of nerve-fibres decreases very rapidly with increasing distance from the nerve entrance. Fresh fibres exhibit many and striking varicosities which are absent from those prepared with chromic acid. The bundles receive filaments from the ganglion-cells.

Connective Frame.

The membrana limitans externa and interna do not exhibit any special characters. The intergranule-layer, which is remarkable for the large scale of its fibres, and the granular layer, have been already described in the order in which they follow the other layers. They are merely mentioned in this place as parts of the connective frame.

The connective radial fibres are disposed differently in the back and front of the retina. Tracing their course from the inner surface of the retina outwards, they arise from the membrana limitans interna by very broad, membranous, winged, decurrent roots, which at the inner surface of the optic nerve-layer contract and form stout pillar-like fibres. In the front of the retina these divide at acute angles, and traversing the intervening layers radially, end at the inner surface of the membrana limitans externa; but in the back of the retina the pillar like fibres in the level of the inner surface of the optic nerve-layer spread like fans, and, in vertical sections, form a series of erect arches in which the

ganglion cells lie. Then splitting quickly into innumerable filaments, they largely contribute to the proper tissue of the granular layer, a few of the stronger filaments reach the outer limit of this layer, and some of these contain fusiform nuclei.

From these terminal branches of the radial fibres coming from the membrana limitans interna, and from the proper tissue of the granular layer near its outer surface, a second system of radial fibres arises. Their roots converge, and form stout pillars which traverse the layer of inner granules and inter-granule-layers, in the level of which they break up, and the resulting fibres proceed between the outer granules to the inner surface of the membrana limitans externa, upon which they are lost. These I term the outer radial fibres, in order to distinguish them from those springing from the membrana limitans interna. In vertical sections they form a series of inverted arches, which rest upon the granular layer, and lodge the inner granules, which are packed in an areolar tissue drawn from these fibres. Receding from the optic nerve-entrance, more of the fibres from the membrana limitans interna traverse the granular layer, and fewer are lost in it; while in the front of the retina, most of them pass through and reach the membrana limitans externa.

Blood-vessels.

Müller believed that he had traced blood-vessels in the retina of the (Schildkrote) turtle as far as the inner granules.* A very careful examination, with particular reference to this, has satisfied me that none exist.

* Müller. Loc. cit.

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In each figure the same layer is indicated by the same numeral :—1, bacillary layer; 2, layer of outer granules; 3, intergranular layer; 4, layer of inner granules; 5, granular layer; 6, ganglionic layer; 7, optic nerve layer; α, membrana limitans externa; β, membrana limitans interna.

Fig. 1.—A Diagrammatic Vertical Section of the Frog's Retina.

1. *Bacillary Layer.*—a, rod-shaft; a′, rod-appendage, or body, connected with an outer granule; b, cone-shaft; b′, cone-body, with an outer granule; b″, a colourless bead in the outer end of the cone-body.

2. *Layer of Outer Granules.*—a, outer granules, each connected with a rod or cone; b, the part of the rod or cone-body which lies inside the plane of the membrana limitans externa; c, pale fibre running inwards from the rods and cones, distinct from Müller's (connective) radial fibres, one of which (d) runs into the membrana limitans externa.

3. *Inter-Granular Layer.*

4. *Layer of Inner Granules.*—a, small cells, deeply stained by carmine; b, large cells, scarcely stained by carmine; c, cells associated with connective radial fibres, δ.

5. *Granular Layer* traversed by the last mentioned fibres, and by other fibres from the optic nerve and ganglionic layers.

6. *Ganglionic Layer.*—a, ganglion cells; a′, fibre going from a cell to the optic nerve layer; a″, fibre proceeding outwards from a cell into the granular layer; a‴, optic nerve fibres passing outwards towards the granular layer.

7. *Optic Nerve Layer.*—Two nerve fibres are represented bending outwards through the ganglionic into the granular layer.

α, Membrana limitans externa; β, membrana limitans interna, at the inner surface of which a blood-vessel containing an oval nucleated blood corpuscle is seen; γ, δ, Müller's connective radial fibres.

Fig. 2.—A Diagrammatic Vertical Section of the Turtle's Retina.

1. *Bacillary Layer.*—a, rods; a′, rod-shaft; a″, rod body, with an outer granule. a, a transverse joint where the shaft and body meet; b, cones; b′, shaft; b″, cone-body, with outer granule in its inner end, and a coloured bead in its outer end, close to the joint.

2. *Layer of Outer Granules.*—a, outer granules, associated with rod and cone-bodies; b, rod and cone-fibres; c, Müller's connective radial fibres.

3. *Inter-Granular Layer.*—Remarkable for the large size of its fibres.

4. *Layer of Inner Granules.*—a, inner granules; b, rod and cone-fibres, with nodal swellings; c an outer set of connective radial fibres, in part arising in the granular layer, in part continuous with the inner set of radial fibres.

5. *Granular Layer.*—The continuity of this with the connective radial-fibres is seen at a a; b, rod and cone-fibres; c, a fibre from a ganglion cell.

6. *Ganglionic Layer.*

7. *Optic Nerve Layer.*

α. Membrana limitans externa, with apertures which receive the rod and cone bodies. β. Membrana limitans interna, with γ the roots of the inner set of connective radial fibres.

Fig. 3.—A Diagrammatic Vertical Section of the Common Snake's Retina.

1. *Bacillary Layer.*—a, a more slender element, possibly to be regarded as a rod; a′, shaft; a″, body, the greater part of which lies inside (α) the membrana limitans externa, in (2) the layer of outer granules, and encloses an outer granule, a. These granules are disposed in a single tier.

3. *Intergranular Layer.*

4. *Layer of Inner Granules.*—a, inner granules packed among the connective radial fibres, d.

5. *Granular Layer.*

6. *Ganglionic Layer.*

7. *Optic Nerve Layer.*

α, membrana limitans externa; β, membrana limitans interna, with the connective radial fibres springing from its outer surface.

Fig. 4.—A Diagrammatic Vertical Section of the Spanish Gecko's Retina.

1. *Bacillary Layer.*—a, shaft; a′, body.

2. *Layer of Outer Granules.*—a, outer granules disposed in a single row lying in the rod-bodies which are continued inwards through the

3. *Intergranular Layer.*

4. *Layer of Inner Granules.*—In this layer the connectiv radial fibres branch at obtuse angles and form a very irregular net.

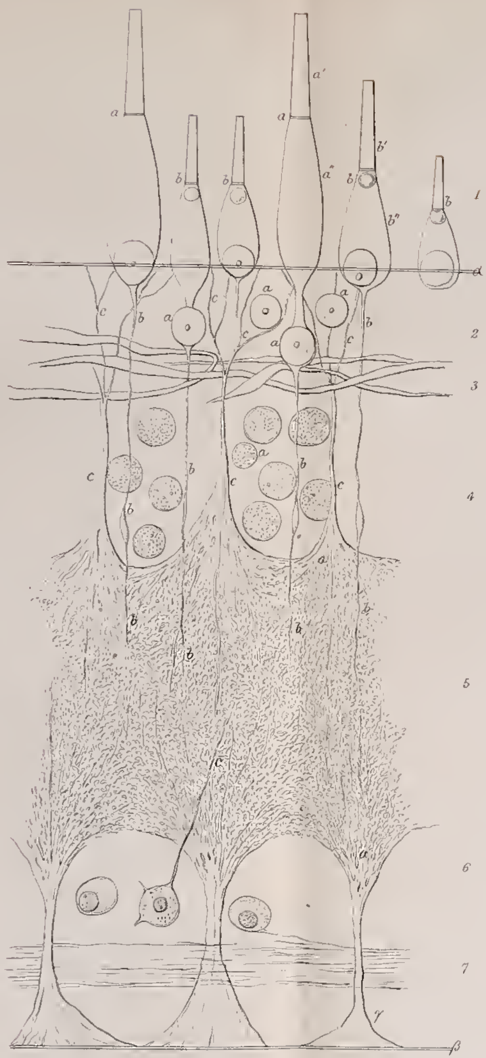
5. *Granular Layer.*—Connective fibres are seen to arise near its outer surface.

6. *Ganglionic Layer.*—a, a ganglionic fibre passing into the granular layer; b, a ganglionic fibre passing to the optic nerve fibres. At the right of the central connective radial fibre two fibres are represented passing from the optic nerve (7) into (5)—the granular layer.

Fig: 1.

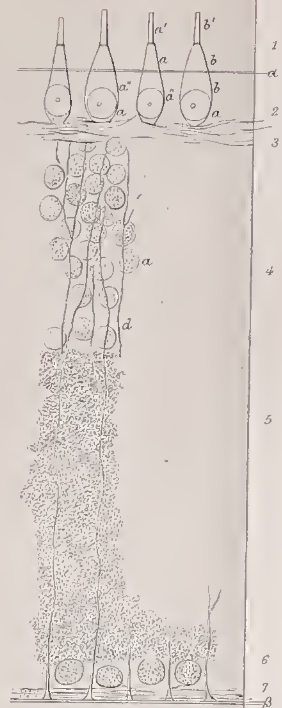
Frog.

Fig: 2.



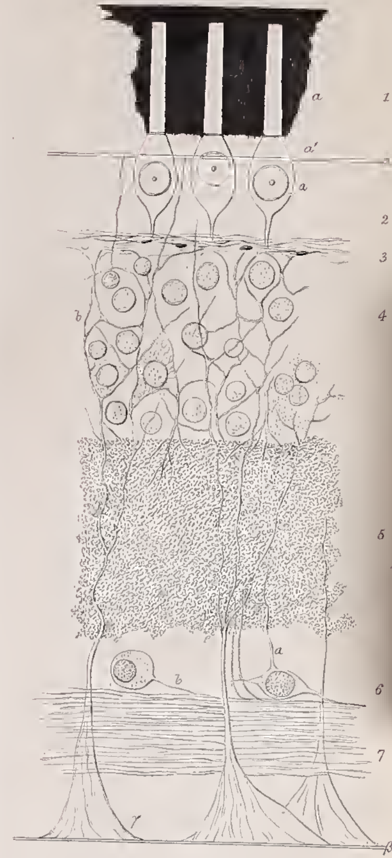
Turtle.

Fig: 3.



Snake.

Fig: 4.



Gecko.

J.W. Hulke del. Tuffen West sc.

W. West imp.